## RESEARCH REVIEW

# Incursion and excursion of Antarctic biota: past, present and future

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## ABSTRACT

**Aim** To investigate the major paradigms of intense isolation and little anthropogenic influence around Antarctica and to examine the timings and scales of the modification of the southern polar biota.

**Location** Antarctica and surrounding regions.

**Methods** First, mechanisms of and evidence for long-term isolation are reviewed. These include continental drift, the development of a surrounding deep-water channel and the Antarctic Circumpolar Current (ACC). They also include levels of endemism, richness and distinctiveness of assemblages. Secondly, evidence for past and modern opportunities for species transport are investigated. Comparative levels of alien establishments are also examined around the Southern Ocean.

**Discussion** On a Cenozoic time-scale, it is clear that Gondwana's fragmentation led to increasing geographical isolation of Antarctica and the initiation of the ACC, which restricted biota exchange to low levels while still permitting some movement of biota. On a shorter Quaternary time-scale, the continental ice-sheet, influenced by solar (Milankovitch) cycles, has expanded and contracted periodically, covering and exposing terrestrial and continental shelf habitats. There were probably refugia for organisms during each glacial maxima. It is also likely that new taxa were introduced into Antarctica during cycles of ice sheet and oceanic front movement. The current situation (a glacial minimum) is not 'normal'; full interglacials represent only 10% of the last 430 ka. On short (ecological) time-scales, many natural dispersal processes (airborne, oceanic eddy, rafting and hitch-hiking on migrants) enable the passage of biota to and from Antarctica. In recent years, humans have become influential both directly by transporting organisms and indirectly by increasing survival and establishment prospects via climate change.

**Main conclusions** Patterns of endemism and alien establishment are very different across taxa, land and sea, and north vs. south of the Polar Frontal Zone. Establishment conditions, as much as transport, are important in limiting alien establishment. Three time-scales emerge as important in the modification of Antarctica's biota. The natural 'interglacial' process of reinvasion of Antarctica is being influenced strongly by humans.

**Keywords**

Alien species, Antarctica, dispersal, invasions, Southern Ocean, species transport.

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## INTRODUCTION

On the Earth of today, continents are large discrete islands of granitic crust surrounded by water. As a result, most marine environments have considerable connectivity, for example with circulation routes north and south of Australia linking the Indian and Pacific Oceans. A large-scale exception to this general connectivity, long recognized by biogeographers, oceanographers and ecologists, is the Southern Ocean. Although the Southern Ocean consists of the most southerly basins of the Atlantic,
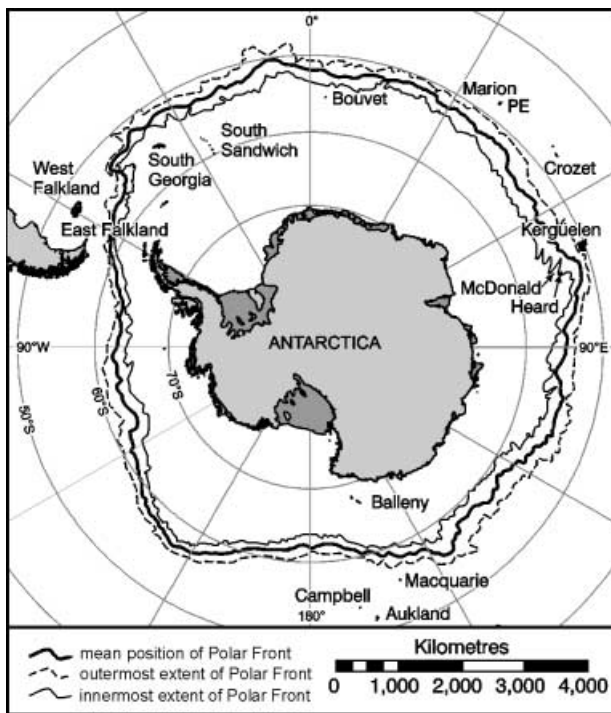
**Figure 1** Seasonal variation in the margin of the Polar Frontal Zone (PFZ), redrawn with data from Moore *et al.* (1999).

Indian and Pacific Oceans, the Antarctic Circumpolar Current (ACC) and its associated fronts create an obstacle to free north–south 'meridional' watermass exchanges. The ACC comprises a series of eastward flowing jets that extend to depths of 3000–3500 m, the strongest of which forms the Polar Front (PF). The path of the PF is controlled strongly by bathymetry but exhibits considerable seasonal and interannual variability (Fig. 1) (Moore *et al.*, 1999). In this paper we use the term Polar Frontal Zone (PFZ) to describe the areas covered by the PF during its annual north–south migration. The discontinuities of temperature and salinity in the PFZ make it an important barrier in terms of both air–sea fluxes and watermass exchanges and, consequently, biogeographical interactions. The Antarctic Circumpolar Current and Polar Frontal Zone isolate Antarctica, its outlying archipelagos and the Southern Ocean from other continents and oceans geographically, climatically, thermally and oceanographically.

Thus, in partitioning the Earth's surface into biogeographical zones, one of the most sharply demarcated regions has always been the Southern Ocean (Hedgpeth, 1969; Dell, 1972; Longhurst, 1998). Most (75–90%) marine invertebrate and fish species present in the Southern Ocean occur only there (Dell, 1972; Arntz *et al.*, 1994, 1997; Angel, 1997; Barnes & De Grave, 2000; Clarke & Johnston, 2003). Since the Eocene cooling < 50 Ma some groups of marine organisms have become extinct in the Southern Ocean (e.g. true crabs and sharks, see Dayton *et al.*, 1994) while others have become much more abundant (e.g. Brachiopoda) and/or species rich (e.g. Pycnogona) than elsewhere. In contrast, on the Antarctic continental landmass, much (although not all) of the fauna has been thought to consist of

Holocene (last 11,000 years) colonists, because previous expansion of ice sheets and glaciers covered the vast majority of terrestrial environments at glacial maxima (Gressitt, 1967; Pugh & Convey, 2000; Pugh, 2003). Yet here, too, there is evidence of the past level of Antarctic isolation in their depauperate and unusual communities (Andrássy, 1998; Marshall & Coetzee, 2000). Such patterns of endemism and biotic richness are but two of a number of pieces of evidence suggesting long-term (*c.* 30 million years) isolation of the Southern Ocean and Antarctic continent by the ACC and PFZ (Clarke & Crame, 1989; Lawver & Gahagan, 2003).

Marine, as with terrestrial, environments may present considerable barriers to species movement (see Myers, 1997), of which the PFZ/ACC boundary to the Southern Ocean is a striking example. Nevertheless, species are constantly 'on the move' — in the air, the sea, hitch-hiking on other objects or organisms and, in the last few hundred years, on a wide array of vectors associated with human activity (Carlton, 1985; Carlton & Geller, 1993). The range of organisms with highly disjunct distributions (for instance, bipolar, montane/alpine) is testament to the long-term success of natural dispersal strategies (see Schofield, 1974; Galloway & Aptroot, 1995). However, the diversity of human vectors and their speed (e.g. ships, aeroplanes) has enabled many species to colonize new regions (see Carlton & Geller, 1993; Bergstrom & Chown, 1999). A species that is moved (as a result of human activity) beyond its natural range or potential area of dispersal is termed a non-indigenous species (NIS) and can (at the time of introduction or later) have major ecological influences. For example, the introduction of Nile perch to African lakes triggered a catastrophic extinction of endemic cichlid fish (Kaufman, 1992), and in NW Europe the arrival of the barnacle *Elminius modestus* on the hulls of flying boats (Bishop, 1947) has been followed by its domination of shorelines and the displacement of native species. Nevertheless, species do make many and massive journeys naturally, either as larvae (Scheltema, 1971) or as adults, for example mites travelling thousands of miles in seabird feathers (Falla, 1960). Rates of introduction and invasion are increasing across the globe (see, e.g. Hewitt *et al.*, 1999). Pugh (2004) estimated that anthropogenic introductions to Southern Ocean islands had outpaced the natural arrival (of spiders) by a factor of 30, while Gaston *et al.* (2003) suggested that human activity had accelerated rates of introduction of NIS to Gough Island (South Atlantic) by 2–3 orders of magnitude.

Non-indigenous species (NIS) are considered widely to be one of the major threats to global biodiversity (Vitousek *et al.*, 1997; McKinney & Lockwood, 1999; Williamson, 1999). Recent analyses have disputed whether invasions are demonstrably a major cause of extinction, but the balance of evidence seems to weigh strongly for a massive effect of invaders (see Gurevitch & Padilla, 2004 vs. Blackburn *et al.*, 2004; Clavero & Garcia-Berthou, 2005). Invaders are particularly recognized as a threat to Antarctic terrestrial communities (Bergstrom & Chown, 1999; Frenot *et al.*, 2005). However, it is becoming clear that scale, both in space and time, and the trophic nature of the invader are important. For example, on a global scale invasions may be driving extinctions but at smaller (e.g. individual island) scales there are

often increases in richness (Sax *et al.*, 2002; Sax & Gaines, 2003). Selmi & Boulinier (2001) showed the importance of spatial issues and regional processes in understanding richness of NIS and native species on the islands surrounding Antarctica. With respect to trophic nature, there is little evidence to link NIS competitors with extinction, at least on short time-scales (Davis, 2003). In contrast, there are many studies showing that introductions of predators are coincident with native species disappearances, especially those of endemic species with small populations (see McKinney & Lockwood, 1999; Jones *et al.*, 2002; Blackburn *et al.*, 2004; Duncan & Blackburn, 2004). However, Blackburn *et al.* (2004) also proposed that extinction patterns are changing, such that most species susceptible to exotic predators have already become extinct and that the dominant pressures on remaining endemics are no longer from introduced predators.

Carlton (1985) considered that > 10,000 species were in transport on any one day. Many potential vectors are available to species for transport even within the southern polar region and across the PFZ and ACC, and the importance of some of these has only become apparent through the application of recent technology such as satellite imagery. Clarke *et al.* (2005) recently questioned the effectiveness of the PFZ as a barrier and discussed the possibility of modern exchanges of organisms between the Southern Ocean and elsewhere. The PFZ clearly represents a barrier of some sort; the question is, how leaky is it? A variety of sources now suggest a multiplicity of vectors, and proven terrestrial, freshwater and marine NIS arrival and establishment even across this 'last frontier' (Bergstrom & Chown, 1999; Lewis *et al.*, 2003; Frenot *et al.*, 2005).

The success of colonization by NIS can depend on a number of factors; attributes of individual NIS (Williamson & Fitter, 1996) and the suitability of the environment (Blackburn & Duncan, 2001) in particular have been suggested from analyses. There are several stages necessary for successful colonization (Ellis-Evans & Walton, 1990; Huiskes & Clarke, 2000; Kolar & Lodge, 2001). Essentially, these can be separated into: (i) long-distance transport from source populations, including the stochastic aspect of arrival at a suitable colonization location at a suitable time of year; (ii) survival after arrival; and (iii) establishment of a long-term reproducing population. The most critical point is not the arrival, but the survival and establishment of invaders. With respect to the establishment of NIS, a particularly pertinent contemporary influence likely to affect all three stages is the current trend of global climate change which, although it has many regional patterns will, in general, act to lower the existing barriers to transport, survival and establishment (Chown & Smith, 1993; Frenot *et al.*, 1997, 2005; Dukes & Mooney, 1999; Convey, 2003). Global Circulation Models vary in the precise detail of their predictions for the Antarctic, but suggest Southern Ocean sea surface temperature rises of the order of 2 K (2 °C) in less than a century (Murphy & Mitchell, 1995). The degree of accuracy at which parts of the Antarctic continent are represented in these models is low, such that areas known to be currently experiencing the fastest rates of change (the Antarctic Peninsula) are not well represented (King *et al.*, 2003), but it is clear that contemporary rates of change in some terrestrial and freshwater environments are among the fastest seen worldwide (Hansen *et al.*, 2002; Quayle *et al.*, 2002; King *et al.*, 2003).

In this review paper we consider the evidence for past and present incursion and excursion of organisms between the southern polar region and neighbouring oceans and continents. We consider the processes that have isolated the Antarctic, the vectors for transportation and how these have changed, the extent and timing of the establishment of NIS, and the spread of such invasions. We focus on a number of case histories and consider how transport and establishment of species between the southern polar region and elsewhere is likely to change in the future in the twin contexts of increased direct human influence and regional and global climate change.

## TIMING AND EXTENT OF ANTARCTIC ISOLATION

When the ancient super-continent of Gondwana started to fragment more than 100 million years ago, major barriers to the movement of terrestrial species were erected. In the near two-dimensional terrestrial environment, geographers and biologists have long been familiar with effective limits to organism movement through barriers such as mountain chains, glaciers, rivers and seas. In contrast, only in the last few decades have ideas of true separation between marine environments developed. The break-up of Gondwana not only created seas and oceans between the drifting continents, but also triggered the formation of marine barriers. These included the isolation of regions of continental shelf, and the development of undersea mountain chains (e.g. mid-ocean ridges), trenches and current systems. Although Antarctica drifted over the southern polar region, the continent's high latitude location, linked inevitably with seasonal periods of complete darkness, did not lead immediately to massive extinction of terrestrial fauna and flora, which remained typical of south temperate regions for a long period subsequently (Clarke & Crame, 1989; Poole & Cantrill, 2001). Even after the commencement of ice sheet formation, the Antarctic experienced periods when this biota could show local expansion, until at least as recently as 8–10 Myr BP. Once the Drake Passage opened (28–23 Ma) and the Tasman Rise had been unlocked from Antarctica (33.5 Ma), a deep water circulation developed from what had previously been shallow circulations, leading eventually to the formation of the ACC and PFZ.

For more than 25 million years the ACC and PFZ have permitted an isolated Antarctica to cool and to develop glaciers, ice sheets and ice shelves. While this isolation has driven the evolution of a distinctive biota, Antarctica is also notable for the biota that failed to survive. Thus, it is the only continent with no brachyuran crabs or balanomorph barnacles in the sea and no trees, molluscs or vertebrates on land. While in the last 100,000–10,000 years mass extinctions of indigenous fauna have occurred on most continents (Vines, 1999), coincident with the spread of humans, Antarctica remained insulated from the 'Anthropocene' until just 2 centuries ago. The Antarctic terrestrial environment, at least, has suffered its own multiple mass extinctions in association with periods of Quaternary glaciation. Until recently it has
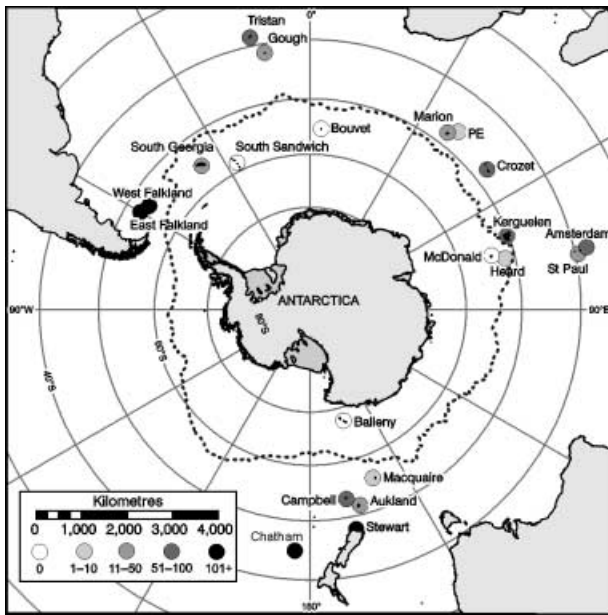
**Figure 2** Vascular plant NIS occurrence in high latitude southern archipelagos. Data from Moore (1983), Dean *et al.* (1994), Vitousek *et al.* (1997), Broughton and McAdam (2002) and Frenot *et al.* (2001, 2005). Data for St Paul Island (Y. Frenot and M. Lebouvier, pers. comm.).

been assumed that the extant terrestrial fauna and flora may be descended from post-glaciation colonists (e.g. see Gressitt, 1967), led by the perception that thicker glaciers and extended icesheets would have covered all lowland terrestrial habitats. However, it now appears that this simplistic view is in need of some modification as an increasing body of evidence indicates that elements, at least, of the terrestrial biota are considerably more ancient in origin (see Convey, 2003, for discussion).

The degree of separation imposed on the southern polar region by the initiation of the ACC and PFZ has been considered typically so robust as to be almost analogous to the closing of the Isthmus of Panama. While biological propagules have crossed (and continue to cross) into the Antarctic (Smith, 1991; Bargagli *et al.*, 1996; Marshall, 1996; Downs, 2003; Whinam *et al.*, 2004), far fewer terrestrial plant NIS are known on islands south of the PFZ than north of it (Fig. 2), although there are, of course, many confounding factors here (not least survival ability and establishment). Terrestrial animal NIS show similar patterns, with much lower numbers on islands south of the PFZ (Table 1). Obviously, resident migratory megafauna, such as birds, seals and whales, are capable of crossing such barriers and have been doing so over macro-evolutionary time, while non-indigenous 'vagrant' species (largely birds) are also recorded regularly, particularly on the isolated sub-Antarctic islands (e.g. Burger *et al.*, 1980; Gauthier-Clerc *et al.*, 2002), where some have managed to establish (Copson & Whinam, 2001). In relation to resident micro- (< 5 mm in size) and macro- (> 5 mm in size) species, various sources of evidence have been used to describe the robustness of oceanographic barriers.

Some marine species (e.g. the sponge *Stylocordyla borealis*) as well as terrestrial mosses, lichens, algae and possibly microbes

have been described as having bipolar distributions (Schofield, 1974; Galloway & Aptroot, 1995; D. Pearce, unpublished data). If these are truly bipolar (rather than being unrecognized cryptic species), they provide evidence for transport on a global scale, far greater than that required simply to cross the PFZ. The terrestrial groups are arguably better-placed for long-distance and trans-global dispersal, as they produce specific highly resistant dispersing propagules which can travel through the extreme but relatively constant conditions at higher altitude in the atmosphere in a dormant state (van Zanten, 1978; Longton, 1988). In contrast, most marine species are faced inevitably with the challenge of maintaining an active physiology through the marine extremes between polar and tropical seas. However, the genetic similarity of some Foraminifera does suggest gene flow through the tropical oceans in recent time (Darling *et al.*, 2000).

## QUATERNARY EVIDENCE

On a scale of tens of thousands of years, both the marine and terrestrial environments of the Arctic have been in a fairly constant state of invasion and reinvasion from temperate regions following glacial expansion and contraction cycles. This faunal exchange is facilitated by the continuous marine and terrestrial connections between polar and temperate latitudes, essentially allowing movement to follow the changing ice edge in both environments. In the Antarctic, similar cycles have resulted in marine fauna being pushed to the edge of continental shelves, followed by recolonization during ice recession (Hodgson *et al.*, 2003). Although there is growing evidence for extensive ice sheets grounded at the slope/shelf break at glacial maxima, the possibility of pockets of shelf refugia cannot be discounted. The level of eurybathy (wide bathymetric ranges, see Brey *et al.*, 1996) and cryptic speciation (Held, 2003) in certain taxa are, for example, suggestive of past shelf refugia.

In the marine environment there appears to be no evidence of movement of species in or out of the southern polar region during recolonization of the continental shelf in interglacial periods. In contrast, the picture on land in the Antarctic appears to be far more complex. While the majority of the historical fauna and flora were driven to extinction in association with glacial cycles, there are strikingly different patterns of distribution between the remaining extant groups. For example, allowing for taxonomic uncertainties, some groups such as terrestrial nematode worms show almost complete Antarctic endemism (Andrássy, 1998), supporting an ancient history, while others, such as the dominant bryophyte vegetation, appear to include no or very few endemic species among their number (H. J. Peat *et al.*, unpublished data), suggesting a much more recent origin in the region.

The most recent geological period, the Quaternary, spans approximately the last 2 Myr BP and is the time during which the polar ice sheets developed their characteristic cycle of slow build-up to full glacial conditions, followed by rapid ice melting and deglaciation to interglacial conditions (Williams *et al.*, 1998). These frequent changes in the configuration of the ice sheets have been driven by the cyclical changes in the Earth's orbital path around the sun (Milankovitch cycles). The most influential of

**Table 1** Numbers of nonindigenous species (NIS) of various higher taxa on archipelagos to the north, on the margins and south of the Polar Frontal Zone (PFZ). The archipelagos north of the PFZ are Gough Island (Gough), Antipodes Islands (Antip), Falkand Islands (Falk), Campbell Island (Camp), Iles Crozet (Croz), Prince Edward Island (PE) and Marion Island (Mar), Iles Kerguelen (Kerg) and Macquarie Island (Macq). South of the PFZ are McDonald Island (McDon), Heard Island (Hear), South Georgia (SG), Bouvetøya (Bouv), the South Sandwich Islands (SSand) and South Orkney Islands (SOrk). Data are from Gressitt (1964), Pugh (1994, 2004), Marris (2000), Pugh *et al.* (2002), Jones *et al.* (2003a,b), Frenot *et al.* (2005), references therein and A. Douse and P. J. A. Pugh (pers. com.). *Does not include Acari

| | North | | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | Gough | Antip | Falk | Camp | Croz | PE | Mar | Kerg | Macq |
| Annelida | | | 1+ | | 2 | 0 | 1 | 3 | 4 |
| Mollusca | 2 | 0 | 3 | 1 | 0 | 1 | 0 | 1 | 1 |
| Chelicerata | 1 | 1 | 6* | 19 | 2 | 3 | 1 | 7 | 47 |
| Crustacea | | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 |
| Insects | 71 | 14 | 6+ | 13 | 11 | 1 | 15 | 21 | 11 |
| Vertebrates | 3 | 1+ | 15 | 8 | 6 | 0 | 1 | 12 | 6 |
| Total | 77+ | 16 + | 32+ | 41+ | 21 | 5 | 18 | 44 | 71 |

| | South | | | | | |
| --- | --- | --- | --- | --- | --- | --- |
| | McD | Hear | SG | Bouv | SSand | SOrk |
| Annelida | 0 | 1 | 0 | 0 | 0 | 1 |
| Mollusca | 0 | 0 | 0 | 0 | 0 | 0 |
| Chelicerata | 0 | 1 | 12 | 0 | 3 | 0 |
| Crustacea | 0 | 0 | 1 | 0 | 0 | 0 |
| Insects | 0 | 1 | 11 | 0 | 0 | 1 |
| Vertebrates | 0 | 0 | 3 | 0 | 0 | 0 |
| Total | 0 | 3 | 27 | 0 | 3 | 2 |

these are the 41-ka (thousand years) obliquity cycle and the 100-ka eccentricity cycle. What is most remarkable about the Quaternary history of Antarctica is that the periods of greatest habitat availability, the interglacials, have been relatively short-lived and unusual. The ice core record from Dome C shows that, in the period 430–740 ka BP when climate variability was dominated by the 41-ka obliquity cycle, the Antarctic has been *c.* 50% in the interglacial phase, although these were weaker interglacials than being experienced at present. However, in the last 430 ka BP, when climate variability has been dominated by the 100-ka eccentricity cycle, the Antarctic has been *c.* 90% in the glacial phase (EPICA, 2004) and some cold periods have been sustained for more than 60 ka (Jouzel *et al.*, 1993). Thus, with only *c.* 10% of the late Quaternary being in full interglacial conditions, for most of this time displacement and retreat of the Antarctic biota, either to refugia or possibly to lower latitudes, appears to be the norm.

As both incursions and excursions of Antarctic biota are taking place actively today then one would expect to find at least some evidence in the Quaternary record. Unfortunately, the constant cycles of expansion and contraction of the ice sheets mean that much of the evidence of past biotas has been 'bulldozed' from the terrestrial oases, nearshore marine sediment basins and continental shelves (Fig. 3). Thus the Quaternary record for the Antarctic is patchy at best. Despite this, there is some compelling, but equivocal, evidence that biota succeeded at crossing into and out of the Antarctic region during this period.

For evidence for the incursion of biota into the Antarctic we look first at the record on land. The largest and deepest lake in the Larsemann Hills, east Antarctica is Progress Lake. On account of its location, on a peninsula known to have been ice free through the Last Glacial Maximum (Hodgson *et al.*, in press), the lake has preserved a sediment record of both the present interglacial (MIS1) and the last interglacial (MIS5e *c.* 115–125 ka BP) (Fig. 4). Ice core evidence shows that MIS5e was warmer than our present interglacial (Jouzel *et al.*, 1993) and that the consequent melting of global ice sheets resulted in a global sea level 5–6 m higher than the present (Lambeck & Chappell, 2001). Remarkably, preserved in the sediments of Progress Lake is an MIS5e diatom flora now characteristic of milder locations including the South Orkney Islands, subAntarctic islands such as Crozet (see van de Vijver *et al.*, 2002), South Georgia, Kerguelen and islands well north of the PFZ such as the Falkland Islands, Macquarie Island and Campbell Island (Fig. 5). With the possible exception of *Diatomella balfouriana*, none of these taxa have been recorded reliably in the continental Antarctic region today (Hodgson *et al.*, 2001). Although currently restricted to one site, this is the first evidence of a present-day subAntarctic community being established in the continental Antarctic during a period when conditions were favourable. As the last glacial period took hold this community was eliminated or displaced and, despite the recent potential for reinvasion by the airspora (Marshall, 1996; Downs, 2003), has not (yet) returned.

Molecular biology can also provide some evidence of the incursion of biota, using 'molecular clocks' to identify where polar affinities have appeared in an organism's evolutionary history. One example is a study of the polar planktonic foraminiferan *Neogloboquadrina pachyderma* using molecular,
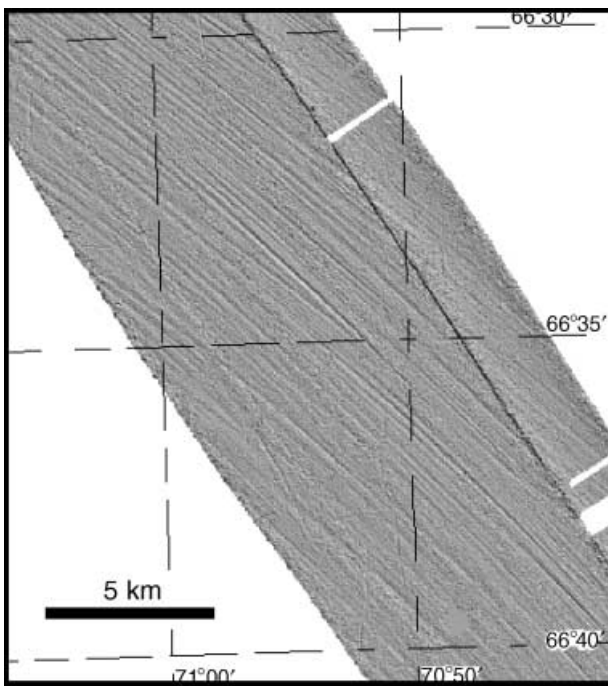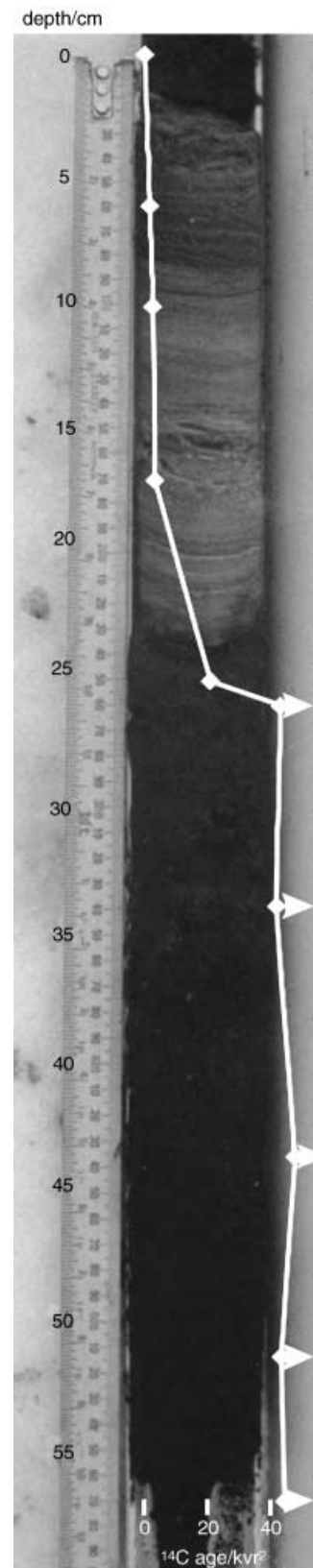
**Figure 3** Bulldozing of the seabed by grounded ice sheets during glacial maxima, evidenced by EM120 sun-illuminated swath bathymetry of the ocean floor. The image shows the mega-scale glacial lineations formed by the grounded palaeo-ice stream that drained the Antarctic Peninsula Ice Sheet, 370 km through Marguerite Bay to the edge of the continental shelf via a bathymetric trough, during the last glacial. The mega-scale glacial lineations are streamlined subglacial bedforms formed by the rapidlly moving grounded ice stream deforming and moulding the sediments. This image shows the ocean floor at a depth of *c.* 500 m. Modified from Ó Cofaigh *et al.* (2002).

biogeographical, fossil and palaeoceanographic data (Darling *et al.*, 2004). Extensive genetic diversity has been discovered within this morphospecies. In particular, the current 'extreme' polar affinity did not appear until late in its evolutionary history, with a stepwise progression of diversification starting with the allopatric isolation of Atlantic, Arctic and Antarctic populations after the onset of the last Northern Hemisphere glaciation, which spanned 115–10 ka BP. Further diversification then occurred only in the Southern Hemisphere and seems to have been linked to glacial–interglacial climate dynamics. These findings show not only the incursion of a new taxon into the Antarctic biome, but also demonstrate the role of Quaternary glaciations in driving the evolution of the modern high-latitude population.

A second and contrasting example is given by a recent study (Allegrucci *et al.*, 2005) of the relatedness of the few species of



**Figure 4** Sediment core from Progress Lake showing evidence of the last two interglacials when the site was ice free (current: MIS1 and the last interglacial MIS5e). Very little deposition occurred during the intervening glaciation as the site was covered by a layer of firnified snow and ice, hence the abrupt switch in the record from the present interglacial to the previous one. White diamonds show the age of the core determined by radiocarbon dating. All dates below 26 cm are beyond the normal (*c.* 45 ka) limit of the radiocarbon method. Modified from Hodgson *et al.* (2003).
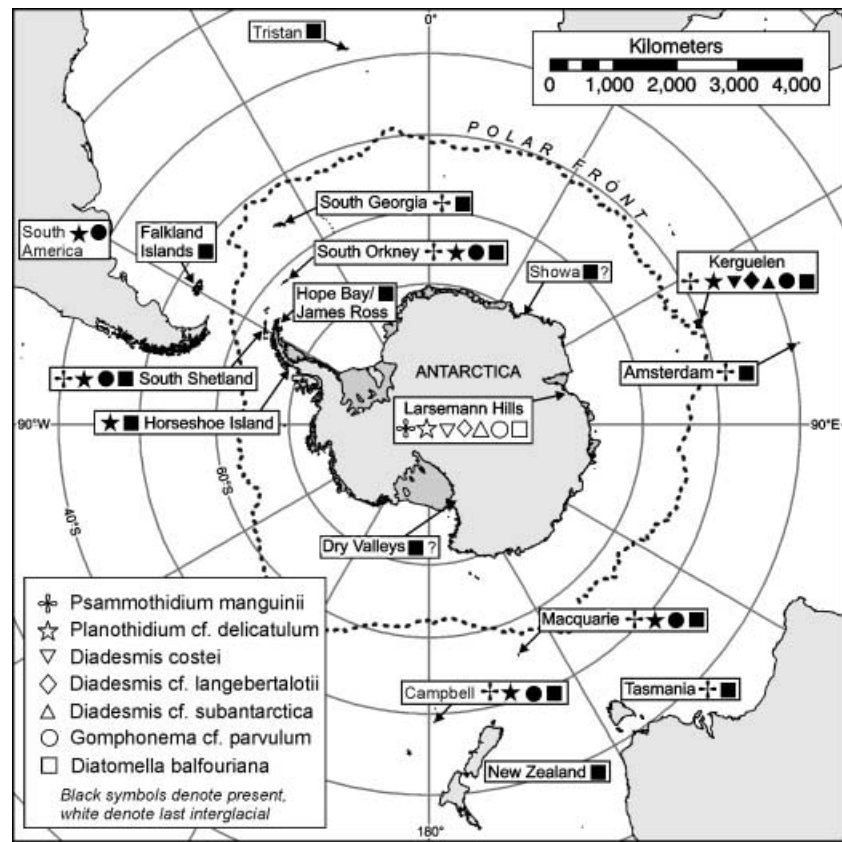
Figure 5 The diatom flora of the Larsemann Hills, East Antarctica, during the last interglacial (MIS5e) and its present-day distribution, based on existing biogeographical and morphological taxonomic evidence.
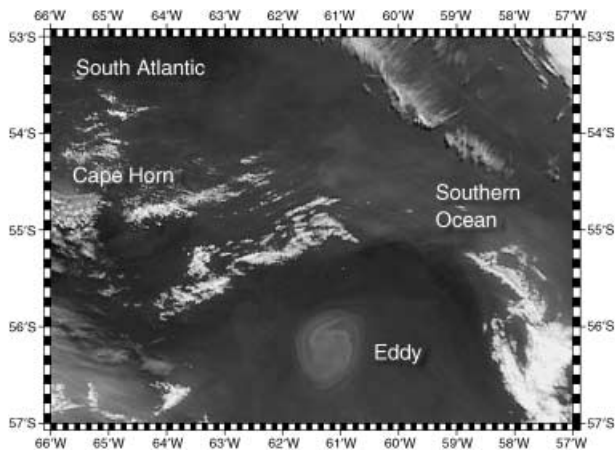


Figure 6 Eddies in the vicinity of the Polar Frontal Zone (PFZ) and the Antarctic Circumpolar Current (ACC).

chironomid midge (Diptera) found in the Antarctic Peninsula region. While inaccuracies in reconstructing histories are inevitable, given uncertainties over true molecular substitution rates, this study illustrates that a species endemic to the Antarctic Peninsula and South Shetland Islands (*Belgica antarctica*) separated from its close relative *Eretmoptera murphyi* (endemic to South Georgia) 35–50 Myr BP, while both separated from southern South American relatives as much as 70 Myr BP. While being the first evidence of this type available for terrestrial species in

Antarctica, this study provides a tantalizing link between the contemporary biology of the Antarctic Peninsula and Scotia arc and its tectonic history, as the currently endemic distributions suggest continuity of existence of these species' evolutionary lines on the tectonic microplates in question.

For evidence of the excursion of the biota from the Antarctic, the marine Quaternary sediment record contains numerous examples of Southern Ocean diatom taxa occurring north of the present-day PFZ (Treppke *et al.*, 1996; Crosta *et al.*, 1998; Romero & Hensen, 2002; Romero & Hebbeln, 2003; Romero *et al.*, 2003; Fenner & Di Stefano, 2004). Similarly, the marine Quaternary record has many examples of temperate taxa occurring in sediments south of the present PFZ (Kopczynska *et al.*, 1998; Zielinski & Gersonde, 2002). Much of these data are equivocal, as it is not clear whether they represent 'crossing' of the PFZ or simply that the PFZ is moving, as it is known to do at present, over deep-basin areas (Moore *et al.*, 1999), or changes in the distribution of sea ice, or that they were transported in meso-scale eddy excursions. What is likely is that taxa with a low thermal tolerance (stenothermal) would be unlikely to survive for long outside of these eddy systems, while others, such as sea ice taxa with wider tolerance to environmental conditions (e.g. salinity, temperature and light availability) might be better suited to survival. For larger pelagic organisms, zoogeographical evidence suggests that their ranges are much more limited by their ability to maintain populations than by any inability to disperse around tectonic or hydrographic barriers to population exchange (Norris, 2000).
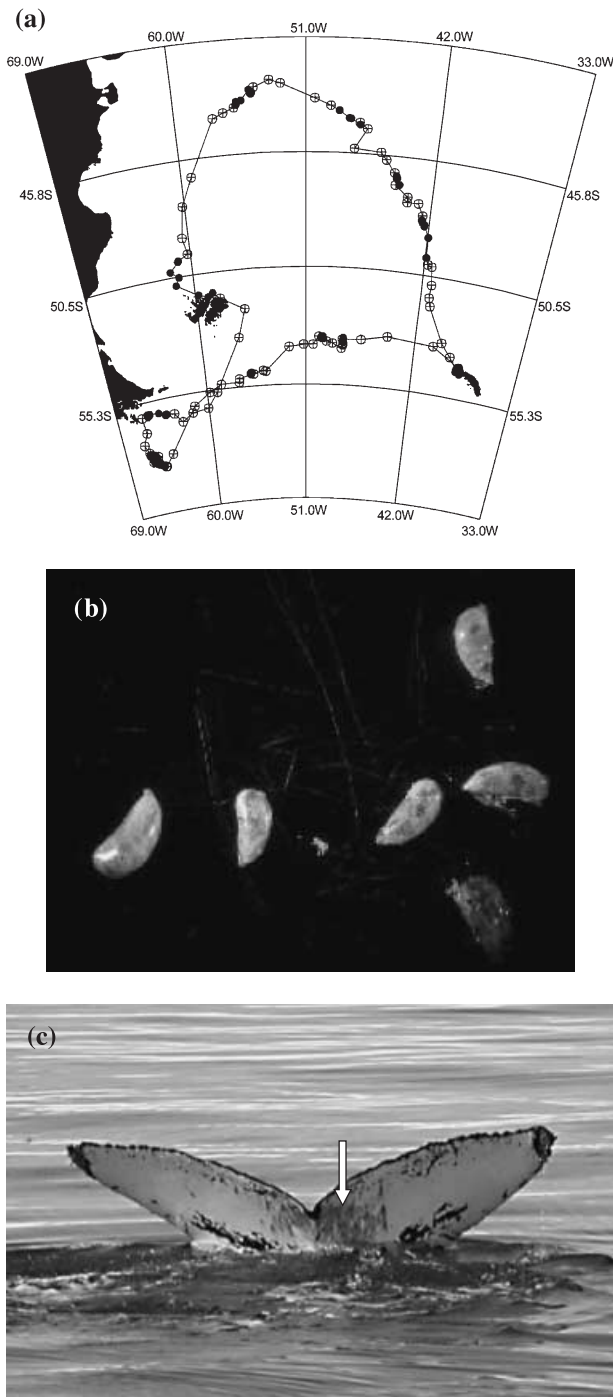
**(a)**



**(b)**



**(c)**



**Figure 7** Marine larvae in flight. An example of a typical journey of a satellite tracked wandering albatross (*D. exulans*) from Bird Island, South Georgia, across the Polar Frontal Zone (PFZ) during the day (open symbols) and night (filled symbols) (Prince *et al.*, 1992) (a). Barnacle cyprids attached to a leg ring from *D. exulans* after return from journey north (b). Diatoms (patches indicated by arrow) attached to humpback whale fluke (c).

Some interesting, but as yet unreplicated, evidence for excursions has also been obtained at the very limit of the present-day mesoscale eddies. Surveys on the south-west coast of Tasmania in the Gordon River estuary in 1993 and 1994 found Southern

Ocean planktonic and sea ice diatom taxa in the water column and sediments (Hodgson *et al.*, 1997). Unfortunately, live material was not examined so it is not possible to say if these communities were alive or simply a result of advection. However, the Southern Ocean taxa present were relatively abundant, with *Fragilariopsis cylindrus* (Van Heurck) Hasle and *F. curta* (Grun. *ex* Cleve) Hasle found at relative abundances of up to 2.5% and 7%, respectively. Other taxa recorded in the estuary include *Nitzschia sublineata* Hasle, *N. angulata* Hasle, *Pinnularia quadreata* Oestrup var. *dubia* Heid., *Navicula valida* Cleve and Grun., *Psammodictyon* spp. and *Thalassiosira australiensis* (Grun.) Hasle. In a related study (Hodgson *et al.*, 1996), evidence for historical incursions into the same estuary have also been found in an 8500-year, 17-m sediment record from a lake now connected to the estuary only by a small creek. At the beginning of this record, before 8500 cal. year BP when the site was part of the early Holocene estuary, the Southern Ocean taxon *Fragilariopsis curta* occurred in relative abundances of 3% at 11 m and 1.2% at 17 m. Even in the relatively recent parts of this record the same taxon occurred in relative abundances of 0.1–1.8% in the top few centimetres, illustrating historic levels of transfer comparable to those seen today.

On land, dispersal studies have, understandably, concentrated on the transfer of propagules into Antarctica (e.g. Marshall, 1996; Whinam *et al.*, 2004). Excursions of Antarctic terrestrial biota are best illustrated by examining the flora of recently formed isolated volcanic islands. The volcanoes forming the South Sandwich archipelago, just south of the PFZ, have maximum ages dating from 0.5 to 3 Ma (Holdgate & Baker, 1979). During this time they have been colonized by a lichen flora that includes 52% of species known otherwise only from more southerly locations in the maritime or continental Antarctic (Convey *et al.*, 2000), suggesting northwards excursion from Antarctic source populations (Convey *et al.*, 2003). These few case studies provide some evidence to support the incursion and excursion of both marine and terrestrial biota into and out of the Antarctic during the Quaternary period.

## EVIDENCE FOR MODERN 'ANTHROPOCENE' INCURSIONS AND EXCURSIONS

Evidence supports limited modern species movement, or the potential for such, in both directions across the PFZ. Among the best examples are the changes occurring on some of the sub-Antarctic archipelagos around the margins of the PFZ (e.g. the Kerguelen archipelago, Frenot *et al.*, 1997, 2001). Being fairly small, isolated, subpolar and having research stations, the richness of these biotas can be both quantified and well monitored. Further north of the PFZ, at Gough Island in the South Atlantic Ocean, more than 70% of the 99 known plant species are established NIS (Gaston *et al.*, 2003). These authors suggested that most human landings may have led to at least one successful invasion. Further south, but still north of the PFZ, Marion Island is one of the better-studied single localities in the world, and more than a third of the vascular plants recorded are NIS (Gremmen & Smith, 1999), with this figure increasing to *c.* 70% in the Kerguelen archipelago (Convey *et al.*, in press).

South of the PFZ most islands have few or no NIS. Only South Georgia, a very large permanently human inhabited island, has many introduced plants (*c.* 50% are NIS), insects, mammals and other taxa. Frenot *et al.* (2005) suggested this was probably related to considerably greater and sustained human activity on this island. Thus, north of the PFZ across the globe, recent colonization/invasion values are typically higher, despite successful attempts to eradicate some NIS (Vitousek *et al.*, 1997). Is the much higher proportion of NIS on islands north than south of the PFZ (Fig. 2, Table 1) a result of different transport opportunities, different controls on NIS survival or establishment relative to indigenous species (Chown *et al.*, 1998; Selmi & Boulinier, 2001), the survival of indigenous species in glacial refugia at some southern locations (e.g. van der Putten & Verbruggen, 2005) or a combination of these factors? Next, we examine the various potential vectors by which organisms may enter into the southern polar biome. These may be categorized into four broad groups.

## At the mercy of currents: aerial and water surface plankton

There is no land bridge between the southernmost margins of the Americas, Africa or Australasia and Antarctica: geography is a major barrier to terrestrial and freshwater species movement. Wind is, therefore, a major vector for the natural colonization of isolated environments, particularly for plants, insects and microbial groups. Preest (1964) suggested that wind dispersal was responsible for vegetating much of the subAntarctic terrestrial environment since the last glacial period and presumably also in previous interglacials. Muñoz *et al.* (2004) have recently drawn a similar conclusion over the importance of aerial linkages in explaining native plant distributions across the Southern Ocean islands. Aerobiological sampling has shown the skies over Antarctica, even at isolated island localities, to contain many terrestrial or freshwater and even some marine propagules (Smith, 1991; Marshall, 1996). At latitudes south of 40° S mean annual wind speeds above the Atlantic, Indian and Pacific oceans are significantly greater than elsewhere worldwide (Bentamy *et al.*, 1996), although are often not appropriate to support north–south transport, as would be required to give the most direct trajectories (Gressitt, 1964; Marshall, 1996). Conditions appropriate for rapid transfer of biological materials from lower southern hemisphere latitudes are relatively infrequent on small timescales. For instance, Marshall (1996) analysed meteorological patterns and suggested that aerial transfer events between South America and the South Orkney Islands might occur as little as once every 18 months. Greenslade *et al.* (1999) and Convey (2005) also used synoptic meteorological data to demonstrate the possibility for occasional rapid transit of living insects between Australia/New Zealand and Macquarie Island, and South America and South Georgia, respectively.

A considerable diversity and abundance of biological material, including pollen, insect scales and propagules of bryophytes, lichens and fungi, have been collected in aerobiological studies on Signy Island (South Orkney Islands), an isolated locality

south of the PFZ (Chalmers *et al.*, 1996; Marshall, 1996; Marshall & Convey, 1997). Marine diatoms (and some pollen) have been found in quantities of up to $3 \times 10^6$ litre$^{-1}$ in snow samples from Rothera Research station at 68° S on the Antarctic Peninsula (C. Allen, unpublished data). The extent of travel of airborne particles around Antarctica is underlined by the regular presence of marine diatoms (some of which originate from north of the PFZ) in ice cores taken at the South Pole (Kellogg & Kellogg, 1996). It seems that many small airborne biological particles can reach the terrestrial habitats of Antarctica in a viable state. In most cases reactivation and establishment remain unlikely to happen, but experimental climate manipulations of terrestrial habitats have demonstrated that conditions more humid or even a degree warmer than currently experienced can enhance propagule growth prospects spectacularly (Smith, 1990; Wynn-Williams, 1996; Day *et al.*, 1999), and illustrate the importance of the extended survival of potential colonists in soil propagule banks. Indeed, the most widely reported response to recent regional climate warming along the Antarctic Peninsula and the maritime Antarctic archipelagos has been a considerable increase in the local ranges and population sizes of native vascular plants (Fowbert & Smith, 1994; Convey, 2003).

Size and mass are major limiting factors for aerial dispersal of organisms. As a vector, therefore, the importance of this dispersal mechanism varies between taxa (e.g. tardigrades are more likely to be carried, and carried further, than non-flying insects and most snails would be too heavy to be carried at all). Large numbers of insects of many species have been trapped at distances far (> 3000 km) from their probable sources (Gressitt, 1964; Bowden & Johnston, 1976). In the 1960s, an array of air sampling nets was set out on Campbell Island to investigate insects being blown to and from the island (Gressitt *et al.*, 1960; Gressitt, 1964). Monthly samples over a 1-year period yielded at least 36 species of arthropod (one crustacean, at least two chelicerates and 33 insects). Some of these were highly abundant, with 970 specimens of a single chironomid midge species (*Exechia hiemalis*) being recorded within the study period, although the methodologies used do not permit assessment of the proportion of these that were alive on arrival. Like many insect groups, spiders also disperse well in wind, particularly those which 'balloon' (extrude fine silk strands). Ballooning spiders were also recorded in the trapping experiment at Campbell Island (Gressitt, 1964) and have been noted further south over continental Antarctica, and away from land over the Southern Ocean (Forster, 1971). Wind has been suggested as a strong explanatory vector for freshwater crustacean distributions, particularly for *Boeckella* sp. (Falla, 1960) and *Daphniopsis studeri* (Laybourn-Parry & Marchant, 1992). In contrast, for terrestrial arthropods and molluscs air dispersal is probably unimportant, except over short distances, in the Southern Ocean or elsewhere (Jacot, 1934; Thornton, 1996; Kirchner *et al.*, 1997; Pugh & Scott, 2002; Pugh, 2003).

A major component of 'aerial plankton' is fungi, but very little information is available on southern polar species and no confirmed NIS are known from Antarctica [although some are suspected; see Kerry (1990), Azmi & Seppelt (1998)]. The Southern polar terrestrial macro-fungi appear similar, even at species level,

to those of northern temperate and arctic regions (Pegler *et al.*, 1980). Similarly, Gray and Smith (1984) found that the Antarctic filamentous micro-fungi they examined were found commonly in temperate soils. Such studies and that of Vishniac (1996) concluded that fungal endemism is very low compared to that for terrestrial biota in general, and especially compared to marine biota. Further, they suggest that Antarctic isolation presents little if any barrier to aerial dispersal of most species, and that the major limitation for fungal colonization of southern polar terrestrial environments is survival. Therefore, despite the discontinuities in land/coast and the isolation of suitable habitats and islands, a major limiting factor for terrestrial colonization by plants, fungi and animals (at least by smaller organisms or those with small propagules) seems to lie in survival and establishment conditions.

Transport on or near the water surface has been suggested as a viable route for certain terrestrial arthropods. Some groups of mites, such as the ameronothroids, include terrestrial, intertidal and marine representatives and species that possess extremely wide ecophysiological tolerances (Marshall & Convey, 2004). Some terrestrial species from both polar regions have the ability to survive long periods of immersion (weeks to months) in both fresh and seawater, and it has therefore been suggested that they are good subjects for transfer either in the water column or on floating debris (Coulson *et al.*, 2002). After mites, the other dominant Antarctic terrestrial arthropod group are springtails (Collembola), and these possess a different ability, that of 'rafting' on the water surface (some prostigmatid mites such as *Nanorchestes* spp. are also capable of this). This ability is clearly utilized in local dispersal between 'islands' of terrestrial habitat (Hayward *et al.*, 2003), while rafts of the species *Cryptopygus antarcticus* have been noted on the sea surface some distance from the coast (Gressitt, 1964). The frequency by which each taxon is transported (propagule pressure) is likely to be a major factor influencing their likelihood of establishment as NIS at high southern latitudes, as elsewhere (Rouget & Richardson, 2003; Whinam *et al.*, 2004).

## Deep water flow, PFZ transgressions and meso-scale eddies: aquatic plankton

For marine species, the principal colonization hurdles are different to those for terrestrial or freshwater organisms, although some (e.g. unicellular algae) are known to be capable of transport in the aerial plankton (Chalmers *et al.*, 1996). At depth (2–5 km), the marine environment of the Southern Ocean is continuous with the southern part of other oceans, but there is little contact at continental shelf depths (< 1 km). Both the PFZ and the ACC form major oceanographic discontinuities throughout most of the water column. About 5 Ma the ocean surrounding Antarctica cooled sufficiently to support sea-ice. Since then dense surface water has downwelled and flowed out from the continent's margins as two major water masses, Antarctic bottom water (AABW) and Antarctic intermediate water (AAIW). AABW, the most dense water mass on Earth, is formed under ice shelves and sea ice close to Antarctica and sinks down the con-

tinental slope into the abyssal basins of the Atlantic, Indian and Pacific Oceans. In contrast, AAIW forms by Antarctic Surface Water sinking at the PF and flowing at intermediate depths (*c.* 1000 m) towards the equator. Both of these water masses have been recorded north of the Equator. Together, they provide an abyssal and mid-depth route through the PFZ to lower-latitude regions of the Atlantic, Indian and Pacific oceans. This is supported, for example, by the finding of *Fragilariopsis kerguelensis* (a southern polar diatom) in deep water in the subtropics (Treppke *et al.*, 1996). AABW moves slowly (about 1 cm s$^{-1}$) along the ocean floor (Hall *et al.*, 1997), and it is unknown whether living cells can survive extended periods in this environment. In comparison, water flow in AAIW, although highly variable, is considerably faster than that of AABW, at about 10 cm s$^{-1}$ (Schmid *et al.*, 2000). Thus, if cells travelled in AAIW, they could emerge at the surface (in the Benguela upwelling system, west southern Africa) after only months (Romero *et al.*, 2003).

The boundary of the PFZ is dynamic in space and time and its position varies more at some longitudes than others (Fig. 1). Moore *et al.* (1999) showed that the PF wandered > 200 km north–south. For example, at its most northerly extent the PF lies at similar latitude to the Kerguelen Archipelago. At its southernmost limit, the PF is > 250 km south of the islands (Moore *et al.*, 1999). When the PF wanders south temperate organisms (e.g. Foramifera, Radiolaria or diatoms) may be deposited. Previously, when the PF lay in a more northerly location, Antarctic species would have been deposited on the same sediment. Analysis of a sediment core at this point could lead potentially to the false interpretation that southern temperate species had penetrated into waters south of the PFZ (or vice versa), when actually the PF had just migrated back and forth.

Considered at the scale of hundreds of kilometres and smaller (mesoscale) the flow of the ACC is complex in direction and velocity. Localized rapid turbulent flow creates temporary but often abundant mesoscale eddies (Gayoso & Podestá, 1996; Froneman *et al.*, 1997; Lutjeharms *et al.*, 2003; Vaillancourt *et al.*, 2003). The energy carried in these eddies exceeds that in the mean flow of the ACC. Eddies may range considerably in size and duration: sizes greater than tens of kilometres are rare, but are typically longer-lived than smaller versions when they do form (Mann & Lazier, 1991). Large eddies have been reported travelling the width of oceans and lasting up to 4 years (Smythe-Wright *et al.*, 1996). The main factors controlling the formation and characteristics of eddies are the ACC velocity and the internal Rossby deformation radius (linked to the Coriolis parameter). The importance of such eddies to the surface oceanography and marine biology of the region has led to a leap in intensity of study and focus upon them, particularly with respect to modelling their creation (Lutjeharms *et al.*, 2003) and ecosystem impact (Pakhomov *et al.*, 2003). Eddies in the region of the PFZ (Fig. 6) can have quite different thermal and chemical properties in their core to surrounding Southern Ocean water (Vaillancourt *et al.*, 2003). The same authors reported viable phytoplankton cells within these eddies. Froneman *et al.* (1997) found the phytoplankton of eddies to be more typical in density and species composition of the location of eddy formation than the waters to

which they were transported. Such eddies make the PFZ porous to transport of plankton both northwards or southwards. Recently, Thatje and Fuentes (2003) found living larvae of benthic crustacean NIS around King George Island in the South Shetland Archipelago, with transport in eddies across the PFZ a likely potential vector (Clarke *et al.*, 2005).

## Transport (hitch-hiking) with other biota or on floating rock or debris

The seeds or fruits of many vascular plants are able to travel considerable (trans-oceanic) distances while remaining viable. Scheltema (1971) has suggested that some marine larvae have similar abilities. These mechanisms have enabled species to colonize emerging shelf environments and oceanic islands such as the many recent volcanic islands (Hawaii and Galapagos archipelagos, Ascension Island, Surtsey and, in the Southern Ocean, Bouvetøya and the South Sandwich archipelago). At lower latitudes rafting on algae, logs, pumice and other floating natural objects (hydrochory) is also widely known, with many terrestrial, freshwater and marine representatives using eggs, larvae or adults as the dispersing stage (Darlington, 1938; Forster, 1955; Winston, 1982; Thornton, 1996; Barnes, 2002). Drifting organic material has been shown to cross the PFZ: Barber *et al.* (1959) found *Nothofagus* tree trunks that had drifted thousands of kilometres to Macquarie Island, and natural driftwood has been noted on shores near the northern (South Sandwich Islands) and southern (Adelaide Island) extremes of the maritime Antarctic (P. C., pers. obs.). Travelling in the opposite direction, Coombs and Landis (1966) found pumice from the 1962 eruptions in the South Sandwich Islands that had crossed the PFZ to arrive on New Zealand shores. Drift card/passive drifter data has proved particularly useful to visualize potential trajectories of floating material and rafting organisms (Thorpe *et al.*, 2004). Clearly, it is possible to traverse the PFZ in either direction even with passive mechanisms. However, the reduced survival chances over the long distances and time-scales involved mean that dispersal of non-marine species on driftwood has been considered by some authors unlikely to be common (e.g. Gressitt *et al.*, 1960).

Few examples of rafting biota have actually been found at high latitudes. Of the known established species that are newly arrived (NIS or naturally dispersed) in the subAntarctic and Antarctic (annelids, chelicerates, crustaceans, insects, molluscs and vertebrates; see Table 1), some are considered likely to have rafted to their current locations. These include some spiders and insects (Forster, 1955 and Gressitt, 1964, respectively), a few snails (Burton, 1963; Vagvolgyi, 1975), at least three species of mites (Pugh, 1994) and probably some crustaceans. The earthworms (*Microscolex* sp.) of the subAntarctic islands are of particular note, as they all have unusually high resistance to salt stress (Y. Frenot, pers. comm.), and it seems likely that this trait would enable these earthworms to be particularly suitable to rafting. Only a few marine species have been recorded rafting at high latitude. These include subAntarctic bivalves, which can travel considerable distances attached to algae (Helmuth *et al.*, 1994). The holdfasts of coastal kelps tend to be rich in attached biota and animals

may survive for considerable periods in such holdfasts, so kelp is an important potential vector for either long-distance travel or dispersal of species after arrival in a locality in subAntarctic locations. Bull kelp (*Durvillaea antarctica*) is particularly buoyant and common: Smith (2002) estimated that, at any given point in time, more than 70 million fronds were rafting in the Southern Ocean Current (at *c*. 50° S).

Every austral autumn large numbers of various marine megafauna (seabirds, penguins, seals and cetaceans) migrate northwards, most across the PFZ — and every spring they return southwards. Their destinations vary and some species regularly carry passengers. Pedunculate barnacles attach to fur (Laws, 1953; Scheffer, 1962) and elephant seals (Best, 1971; Arnbom & Lundberg, 1995) while north of the PFZ and are still attached on their return to subAntarctic island shores. One species of stalked barnacle, *Lepas australis*, is found attached to *c*. 4% of female fur seals arriving at Bird Island, South Georgia, every spring (Barnes *et al.*, 2004). These authors state that the trans-PFZ hitch-hiking *L. australis* fall off dead a few days after the seals haul themselves up onto the shore. However, the migrating megafauna provide a fast route through the PFZ for any stalked barnacles, which arrive mature enough to release larvae. Furthermore, the barnacles themselves provide hard surfaces for potential fouling species to colonize and hence also be transported. Barnes *et al.* (2004) also report adult barnacles on a macaroni penguin and barnacle cyprid larvae on the feet of a wandering albatross (*Diomedia exulans*). Aquatic migrant animals such as whales also act commonly as long-range vectors for organisms such as diatoms (Fig. 7c).

Birds have long been considered important vectors for the spread of freshwater species. Several Southern Ocean species, including *D. exulans*, cover massive distances rapidly, including those between Antarctica and other regions (Fig. 7). Albatrosses and other similarly behaving species do not visit freshwater or generally any land other than their breeding sites, so are likely to be a potential vector only for marine species. Birds are often assumed to be vectors for transfer of terrestrial biota into Antarctica, many of which would be unable to survive the combination of stresses experienced during independent transport through the marine or aerial environment (in particular, low temperature, desiccation, pressure during diving and salinity). However, there are very few explicit demonstrations of such transport, and these are limited to a small number of algae and microbiota (Gressitt, 1964; Schlichting *et al.*, 1978). The Antarctic (especially the subAntarctic islands) harbours large populations of many pelagic bird species. Virtually all such species leave the Antarctic continent and Peninsula in winter, as do a significant proportion of the subAntarctic populations. The most plausible vector species are those whose migrations bring them into direct contact with other continental landmasses, often through their tendency to forage around sites of human activity (e.g. farming and refuse areas). In this context, species of skua, gull and sheathbill are likely to be of far greater importance as vectors of terrestrial biota than penguins, seals, albatrosses and petrels. Vagrant birds from southern continental land masses, such as cattle egrets, are also likely to be important potential vectors. Finally, viable terrestrial mites have also been found in the guts of seals (Pugh, 1994), and

Pugh (1997) also reviews the potential role of zoohoria (inadvertent animal vectors) more generally in the transport of terrestrial invertebrates into the Antarctic.

Plants may disperse over considerable distances using vertebrates to carry their seeds in their digestive systems. It is likely that some NIS plant species arrived on South Georgia and other subAntarctic islands within introduced vertebrates and colonized from dung (Headland, 1984; Frenot *et al.*, 2005). Similarly, most new plant species to arrive at Gough Island originated from seeds found in bird droppings (WCMC, 1994). The ability of animals to pass through the guts of other animals, thereby gaining dispersal advantages, is much less well known (see Chmielewski, 1970), although the morphology of some organisms, with tightly sealed shells or resistant life stages, renders them resistant to digestive enzymes. For brooding marine invertebrates, such as the bivalve *Mysella charcoti*, survival of passage through a highly mobile host (the fish *Notothenia coriiceps*) provides a vector to a species of otherwise severely restricted movement (Domaneshi *et al.*, 2002). While *N. coriiceps* is unlikely to cross the PFZ, many birds and seals do so regularly. Diatoms are a further group that may survive passage through the guts of some animals.

## Anthropogenic transport

Coincident with human arrival on other continents and islands across the globe, there have been waves of introduction, establishment and demographic spread of terrestrial, freshwater and marine NIS. Concurrently, there have been large-scale decreases of native fauna, and particularly endemic species and larger organisms (Vitousek *et al.*, 1997; Vines, 1999; Blackburn *et al.*, 2004). As a result of many inter-related factors changing with human activity (e.g. hunting/fishing and habitat destruction), it is difficult to partition the contributions of the various anthropogenic pressures to such extinctions. In contrast, in Antarctica and the Southern Ocean the known major extinctions of native taxa (e.g. terrestrial vertebrates, subfossil penguin species) happened long before human activity in the region. However, there are examples of local extinctions, for instance of populations of burrow-nesting bird species on islands within subAntarctic archipelagos subject to rodent introduction, while populations on pristine islands in the same archipelagos persist (see Frenot *et al.*, 2005 for review). In parallel with influences on other continents, and coincident with the timing of human arrival, there has been both a major decrease in populations of large mammals in the Southern Ocean (through commercial fisheries for whales, elephant and fur seals) and introductions of NIS to the terrestrial environment. A wide diversity of anthropogenic vectors exists, from passive rafting on floating synthetic debris, fouling the hulls of ships, uptake with collection of ballast water by ships, in live plants (often fruit and other fresh produce for human consumption), on untreated wood and brought in or spread directly by humans (either accidentally or deliberately) (Chown & Gaston, 2000; Whinam *et al.*, 2004; Frenot *et al.*, 2005).

In the early 1980s, plastics and other synthetics began to be found floating and stranded on shores in the Southern Ocean (Gregory *et al.*, 1984). Since then, over the last few decades the amount of synthetic material entering the world's oceans and washing up on strandlines has increased drastically. Rapid build-up of drift plastic has even been recorded on remote, uninhabited islands such as Inaccessible Island in the Tristan da Cunha archipelago (Ryan & Moloney, 1993) and subAntarctic Prince Edward Archipelago (Ryan, 1987). Plastics landed on the shores of some of the South Sandwich Archipelago, south of the PFZ, even before humans had landed on them (Convey *et al.*, 2002). In the tropics up to half the floating plastic has been found to carry hitch-hiking biota, but this reduces to < 1% at high southern latitudes (Barnes, 2002). Nevertheless, on the shores of Macquarie Island, on the margins of the PFZ, hitch-hiking barnacles on (mainly fishery-related) drift plastic can be a significant source of food for seabirds (Schulz & Burton, 1991). Recently, Barnes and Fraser (2003) found five phyla of marine organisms attached to a floating plastic packaging band south of the PFZ. Although these taxa were all Antarctic endemics, some individual colonies were more than a year old, demonstrating that a diverse range of hitch-hikers can survive a winter on the surface of the Southern Ocean, as well as illustrating the potential for intra-regional transfer of biota.

Shipping has probably been a vector for transporting organisms for thousands of years, and ports are typically the richest localities of marine NIS (e.g. Hewitt *et al.*, 1999). Wonham *et al.* (2001) found at least 50 species in the ballast water of a vessel on a 16-day transAtlantic crossing (although only < 2% of individuals survived the voyage and ultimately none were estimated to survive release). Shipping is thought to be the predominant anthropogenic method of global marine species transport, mainly through carrying ballast water from place to place and releasing it (Carlton, 1985, 1987) but also through organisms attaching to the hull (fouling) (Thresher, 1999). Global shipping patterns are not changing markedly (although northern shipping routes are likely to assume greater importance with continuing reduction in Arctic sea ice formation and duration — Convey *et al.*, 2003). Those at some Southern Ocean localities are rapidly increasing (Frenot *et al.*, 2005), although such an increase is from a lull in the late 1900s. From the 1800s to the mid-1900s shipping levels in the Southern Ocean would have been considerable (if poorly documented) due to the sealing and whaling industries.

Lewis *et al.* (2003) show that, in the Southern Ocean, transport by ships differs in its effect and directionality from elsewhere for a number of reasons. First, the overall level of shipping is very small because no major trade routes cross the Southern Ocean. Secondly, the carriage of cargo is (relatively) small and so, therefore, is the requirement for ballast water. For example, tourist ships, which constitute *c.* 20% of Southern Ocean shipping, have little reason for exchange of ballast water. Thirdly, ballast water would usually be taken on by national operators' ships northbound from Antarctica, after discharge of cargo to Antarctic stations. Thus movement of species in ballast water is virtually all likely to be excursion from Antarctica (rather than bidirectional). For instance, inspection of sludge from the base of the ballast tanks of the United Kingdom's research vessel RRS *James Clarke Ross* on return from the Antarctic revealed many Antarctic

diatoms (C. Allen, unpublished data). In contrast, transport of fouling communities will only be in the opposite direction (southwards). As Lewis *et al.* (2003) identify, the first (in each year) voyage south for each visiting ship is likely to be the only major risk for introduction of NIS to the Southern Ocean. Fourthly, although antifoulant paint can be removed quickly by ice abrasion, so would be any settling biota. The very limited inspection data available of research ships on arrival in the Antarctic reveal hulls devoid (D. K. A. B., pers. obs.) or depauperate (Lewis *et al.*, 2003) of fouling fauna. Lastly, it has been suggested that the (rapid) speed of transport of ship fouling communities across a major thermal discontinuity (the PFZ) would provide some defence through being a considerable source of heat-shock stress (*c.* 5 K in an hour) to potential NIS (Barnes, 2002). Many tourist vessels do not have double-skinned hulls, and thus insulate poorly any biota carried in ballast water from changing external sea temperatures. Ballast water taken up in the Southern Ocean and released north of the PFZ would present considerable shock to typically highly stenothermal Antarctic biota (cf. Peck, 2002). Nevertheless, ships are potentially significant sources of introduction (Lewis *et al.*, 2003) and have been suggested as the sources for the two Antarctic marine NIS known to date (Clayton *et al.*, 1997; Tavares & Melo, 2004).

A virtually unstudied, but clearly potentially significant, source of anthropogenic introduction is via air transport. The major routes for aircraft traffic into Antarctica are from Christchurch, New Zealand, to McMurdo Station, continental Antarctica (Ross Sea coast), from Stanley (Falkland Islands) to Rothera, Adelaide Island and from Punta Arenas (Chile) to King George Island (South Shetland Islands). Smaller operations are conducted from Cape Town and Hobart to the continental Antarctic coast and from Punta Arenas to the Patriot Hills (Ellsworth Mountains). Such routes enable fast, direct access for brief duration life stages, with anecdotal observations confirming transport of dipterans southbound into Antarctica and, following survival within the aeroplane fuselage, northbound back to the point of origin (S. Ott, P. C., pers. obs.). Convey *et al.* (2000) and Frenot *et al.* (2005) also highlight the potential ease of accidentally transporting terrestrial species from one region of Antarctica to another with the many intraregional flights (and shipping visits) between stations and to field sites. The risk with such transfer is that species are likely to have a much greater chance of establishment, coming from not-dissimilar environmental conditions, while detection of its occurrence is likely to be difficult.

Anthropogenic introduction is suspected as typically being the principal vector conveying most species to new localities to date (Chown *et al.*, 1998; Frenot *et al.*, 2005; but not for mites, see Pugh, 1994). This is even the case for taxa such as the freshwater Crustacea (McKenzie & Moroni, 1986), for which no anthropogenic introductions to the southern polar region are clearly established (but many suspected; see Pugh *et al.*, 2002). A common source of introduction of NIS to the southern polar region is probably on live plants (e.g. see Burn, 1982). In a single event in 1990 at Tristan da Cunha Island, 10 species of snail, two insects and some mites were present in a single imported cauliflower (WCMC, 1994). Some NIS are able to become established only within the confines of areas of continued human activity. For example, the cockroach (*Blatella germanica*) introduced to South Georgia only survived (although abundantly) around the active whaling stations and died out when these were abandoned (Headland, 1984). More recently, midges became established in the sewage tanks at Casey station on the continental coast for 6 years before being eradicated. Although few published data exist, there are many anecdotal records of such introduction and, occasionally, long-term establishment of a range of invertebrates within the environs of Antarctic research stations (Hughes *et al.*, 2005).

Many NIS have been introduced deliberately to subAntarctic islands by humans. Typically these include edible or aesthetic plants, vertebrates (birds and mammals) and even parasites (including viruses) to control previously introduced pests (Sobey *et al.*, 1973; Skira *et al.*, 1983; Frenot *et al.*, 2005). Most deliberate introductions were carried out on subAntarctic islands north of or on the margins of the PFZ, generally to make them more inhabitable to settlers or for passing whalers, sealers and fishermen. Many of the birds and mammals introduced deliberately will have carried other NIS either on their bodies or in association with forage material. However, it is notable that even relatively recently, NIS have been introduced south of the PFZ both deliberately and accidentally in scientific transplant experiments (Holdgate, 1964; Edwards & Greene, 1973; Block *et al.*, 1984).

## ANTARCTICA'S NONINDIGENOUS SPECIES

Most of the individually recognizable and known NIS to have established in the southern polar region are vascular plants (Frenot *et al.*, 2005; list 108 — nearly all angiosperms and mostly perennial). Two major subAntarctic islands remain free from vascular plant NIS: McDonald Island and Ile Pingouins (in the Crozet Archipelago) (Fig. 2, see also Dreux *et al.*, 1988; Jenkin, 1997). Most of the vascular plant NIS to have become established have done so at just a few islands of a single archipelago, but some (approximately six) are distributed widely, including the invasive grass species *Poa annua* (see Frenot *et al.*, 1997, 2001). Plants of *P. annua* have even established on maritime Antarctic islands close to the Antarctic mainland (Deception and King George islands in the South Shetland archipelago), although being wiped out subsequently from the former by a volcanic eruption (Smith, 1996). Such species have become significant space occupiers on some subAntarctic islands and thus represent a potential threat to native and endemic plants (Gremmen, 1997; Gremmen *et al.*, 1998; Ryan *et al.*, 2003; Convey *et al.*, in press). Whether or not the local scale reductions resulting from these competitive invaders would generally lead to extinctions of native species is unclear (Sax *et al.*, 2002; Davis, 2003).

Most vascular plant NIS on Antarctica's outlying islands have remained close to sites of human occupation, almost certainly their sites of introduction. Although most of the successful species are wind dispersed (see Gremmen, 1997), some also produce seeds adapted to attach to passing vertebrates. Some NIS plants present are insect-pollinated at lower latitudes [e.g. bird's foot trefoil (*Lotus corniculatus*) and umbellifer species (Apiaceae) found on South Georgia], but there are currently no pollinating

insects present at their Antarctic location. Thus, the future establishment of pollinating insects could have a secondary 'doubling effect': not only would an NIS insect establish and spread but it could aid the spread of an already established plant NIS. South of the subAntarctic islands, few vascular plant NIS have established (Smith, 1996) and none have been reported in continental Antarctica. There appear to be no confirmed instances of non-vascular plant NIS (i.e. mosses, liverworts, lichens), and also no clear examples of species showing distributions obviously centred on locations of human activity. Lindsay (1973) suggested that a number of lichens on South Georgia were introduced and Ochyra *et al.* (2003) proposed similarly that the moss *Thuidium delicatulum* may have been introduced to Marion Island. This is an area in need of urgent attention. Similarly, very limited data are available illustrating the occurrence of microbial NIS (Wynn-Williams, 1996; Kashyap & Shuka, 2001; Minasaki *et al.*, 2001) but, again, few coherent studies have been attempted.

The majority of animal NIS known to date are insects, more specifically Diptera (flies), Collembola (springtails) and to a lesser degree Hemiptera (bugs) and Coleoptera (beetles) (Frenot *et al.*, 2005). Insects also dominated Gressitt's (1964) array of sampling nets at Campbell Island both in terms of numbers of individuals and numbers of species. However 50–80 Acari, 12 molluscs, seven annelids and many crustaceans are suspected or confirmed to date as NIS to the southern polar region (Pugh, 1994; Smith & Stanisic, 1998; Pugh *et al.*, 2002; Frenot *et al.*, 2005; and references therein). As a result the native invertebrates on such islands are considered to be highly vulnerable (Chevrier *et al.*, 1997; Jones *et al.*, 2002). South of the PFZ, South Georgia is the main locality where terrestrial or freshwater invertebrate NIS have established and spread. In a few cases, NIS beetles (e.g. *Trechisibus antarcticus*) and flies (e.g. *Calliphora vicina*) are having a pronounced influence on indigenous species (Ernsting *et al.*, 1999 and Chevrier *et al.*, 1997, respectively). Many mites are suggested anecdotally to have been introduced to maritime and continental Antarctic sites but in total only a few (*c.* 3) terrestrial species of all taxa combined are known to have become established (see Frenot *et al.*, 2005 for a recent review).

In the last decade there have been major (and mostly successful) efforts to minimize or eradicate the influence of NIS on native organisms on small islands around the globe (see Chown *et al.*, 1998; Chapuis *et al.*, 2001; Bester *et al.*, 2002). At high southern latitudes vertebrate NIS have been mainly mammals and birds, of which cats and rats have had the greatest ecological impact (Pascal, 1980; Bonner, 1984). South of the PFZ, only at South Georgia have vertebrates become established. NIS birds in the southern polar region are often species that are invasive elsewhere, and are likely to have reached subAntarctic islands by natural transfer following their earlier introduction to temperate Southern Hemisphere sites. Some fresh water fish (salmonids, e.g. the brown trout) have been introduced and become established on islands north of the PFZ.

No marine animal NIS are proven to have established in the Southern Ocean to date. Ralph *et al.* (1976) found a single specimen of a mussel (reported as *Mytilus edulis*) at Grytviken harbour, South Georgia. More recently, there have been three recent reports of marine NIS transported across the PFZ in the last decade (Clayton *et al.*, 1997; Thatje & Fuentes, 2003; Tavares & Melo, 2004). None of these species have been recorded in more than one life stage or on more than one occasion. Although no marine NIS are yet established demonstrably, the Southern Ocean seems likely to follow the pattern seen elsewhere over time.

## SUMMARY AND CONCLUSIONS

A range of valid barrier mechanisms have provided various degrees of isolation to both the Antarctic marine and terrestrial environments throughout the evolution of the continent. However, as this paper has described, the generally prevailing 'isolationist' view is over-simplistic and now requires important areas of modification. We can identify three critical time-scales over which the biota of Antarctica and its surrounding Southern Ocean have been modified by exchange with elsewhere.

The first is the very long time-scale of the Cenozoic. During the last 65 Myr Antarctica has become increasingly isolated by distance from the other fragments of Gondwana, and since about 25–30 Myr BP even more isolated by the inception of the ACC. At the same time, seawater in high southern latitudes has gradually (but non-linearly) cooled from warm temperatures in the early Cenozoic to contemporary polar values. Associated with this have been a number of notable extinctions, including those of most reptant decapods, reptiles, cartilaginous fishes and many teleost fishes (Dayton *et al.*, 1994; Aronson & Blake, 2001). Prior to the inception of the ACC, exchange of shallow-water biota with nearby areas (and especially the Magellan province of southern South America) would have been extensive, as is shown in the strong faunal relationships that remain between the shallow-water Magellan and Antarctic biotas (Dell, 1972; Glasby & Alvarez, 1999; Barnes & De Grave, 2000; E.E. Boschi & M.A. Gavio, unpublished results). Once the ACC had formed, however, such free exchange would have been severely curtailed by the associated frontal systems. Modern data, however, suggest that faunal exchange has continued at a low level, facilitated by eddy formation and transport. The continued cooling of the Southern Ocean, has significantly reduced the possibility of establishment for new arrivals.

It would be informative to document the continuing exchange between Antarctic and elsewhere by following the evolution of the fauna through the Cenozoic. Unfortunately, the fossil record of Antarctica is too patchy in space and time to allow this, although studies of molecular evolution provide a potential alternative route and have already generated some tantalizing data. Evolutionary processes are particularly difficult to follow in the terrestrial environment. Here, the limited extant fossil record does support the presence of cool temperate vegetation and vertebrate and invertebrate fauna, well after the final processes of separation from South America commenced. On an evolutionary time-scale, it even allows very general conclusions to be drawn over the movement of biota (e.g. marsupial mammals) from Australia towards South America, before the respective land connections broke. However, this record is too fragmentary to allow detailed conclusions to be drawn over patterns of ingress and egress of biota.

The second time-scale of interest is associated with Milanko-vitch-driven fluctuations in the size and extent of the continental ice-sheet. The climate signal has at some periods been dominated by the 40-ka obliquity cycle and at others, such as today, by the 100-ka eccentricity cycle. It is believed that the Antarctic continental ice-sheet will have responded to this climate variability, both directly or through sea-level changes driven by the response of the smaller Northern Hemisphere ice sheets, or by variation in extent and by responses to global changes in atmospheric $CO_2$ that account for the north–south synchronization of glacial periods. These variations will have resulted in periodic coverage and exposure of terrestrial and lacustrine habitats on land, and of the marine continental shelf. Although the length of time for which Antarctica has been glaciated suggests that there have been many fluctuations in ice sheet extent, reconstruction is complicated by the tendency for each glacial maximum to eradicate evidence from previous ones. Nevertheless, current biogeographical and phylogeographical evidence suggests that there were some refugia for terrestrial organisms, even at the height of the Last Glacial Maximum (Hodgson *et al.*, 2001; Cromer *et al.*, 2005; Allegrucci *et al.*, in press). Conceptually, the problem of identifying refugia locations or mechanisms applies equally if not more so to marine (continental shelf) biota. While evolutionary evidence (endemism, diversity) argues strongly for isolation throughout this period, there is little evidence of refugia for continental shelf benthos. The extended bathymetric ranges of many benthic taxa in Antarctica (Brey *et al.*, 1996) and also the recent demonstration of speciation along depth gradients (K. Linse, unpublished data), suggest that the continental slope beyond the ice sheet grounding line at the shelf-break may have been a key refugium. Whether refugia were also to be found on the shelf is unknown at present. It is believed currently that periodic contraction of ranges to refugia followed by expansion to newly uncovered habitat will have driven speciation in many taxa (Clarke & Crame, 1989). However, evidence is starting to accumulate that the periodic ice sheet extensions may have been accompanied by shifts in the position of the ACC and associated fronts. This may have acted to introduce new taxa into Antarctica, but this is difficult to demonstrate from fossil evidence at present and resolution, as with the terrestrial biota, may have to await molecular phylogeographical studies.

The third time-scale is that of ecology, and involves processes such as range expansion, dispersal and establishment of new taxa. It is now clear that there are many natural processes introducing new taxa into Antarctica, and also taking taxa north from Antarctica into subpolar regions. Current data suggest that the factors limiting establishment of viable populations are often those associated with survival and growth after arrival, rather than transport itself. On this time-scale, humans have recently introduced changes in two important aspects: first, by directly aiding transport and secondly, indirectly through the anthropogenic processes that have led to the recent and continuing trends of climate change. The former will increase the number and range of taxa arriving in Antarctica, whereas the latter will most probably increase the probability of survival and establishment.

The contemporary pattern of NIS discovery, introduction and establishment is, overall, likely to increase, and probably far outweigh the magnitude of natural processes. Predicting which invaders will survive transportation and establish, spread or become ecological 'pests' remains, as elsewhere, very difficult (Kolar & Lodge, 2001; Greenslade, 2002).

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## BIOSKETCHES

**David K. A. Barnes** is a marine ecologist, based at the British Antarctic Survey, investigating coastal environments, primarily in the Antarctic and Arctic. He, together with colleagues and PhD students, is trying to understand current patterns of coastal richness, community dynamism in space and time and influences on these such as competition and disturbance. To do this, specific taxa were chosen as models, such as hermit crabs, demosponges, echinoids and bryozoans in different regions.

**Peter Convey** is a terrestrial ecologist at the British Antarctic Survey. He has wide-ranging interests, including developing understanding of how organisms adapt to the most extreme polar environments and how they respond to the challenges of both natural environmental variability and anthropogenic climate change, and understanding the contemporary and historical processes underlying patterns that can now be seen in Antarctic biogeography.

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